

Fish dynamics in a coastal food chain: Simulation and analysis

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ABSTRACT

This paper presents a model for simulation of fish biomass in coastal waters. The main fish processes simulated are adult growth, mortality, movement, spawning, and larval recruitment. The simulation is integrated into a large-scale ecological model, which includes physical processes and food-web interactions. An object-oriented framework has been used as a development platform.

Some results are presented which provide insight into the population dynamics and distribution of a pelagic species, *Engraulis encrasicolus* (Linnaeus, 1758). The transfer of biomass through the food chain is analysed with the model, and some speculations are made concerning the type of feeding control found in this ecosystem.

By analysing the capture of adult fish in the estuary, and the dynamics of the juvenile population, the direct and indirect value of ichthyofauna in the system has been estimated. This is important in determining the 'ecosystem value' of the resource.

The model was also used to test the impact on fish populations of different development scenarios. Potential nutrient increases due to urban growth on the southern shore of the estuary were compared to the reference situation, and impacts of increases in fish stock were examined.

Key words: Ecological modelling, fish, population dynamics, estuary, coastal waters, management.

RESUMEN

Dinámica ictiológica en una cadena trófica costera: simulación y análisis

Este trabajo presenta un modelo para la simulación de una biomasa ictiológica en aguas costeras. Los principales procesos ictiológicos simulados aquí son crecimiento adulto, mortalidad, movimiento, desove y reclutamiento larval. La simulación está integrada en un modelo ecológico a gran escala que incluye procesos físicos e interacciones de la red trófica. Un marco objeto-orientado ha sido usado como plataforma de desarrollo.

Se presentan resultados que proporcionan un conocimiento de la dinámica de población y distribución de una especie pelágica, *Engraulis encrasicolus* (Linnaeus, 1758). Con el modelo, se analiza la transferencia de biomasa a través de la cadena trófica, a la vez que se especula acerca del tipo de control trófico en este ecosistema.

Ha sido analizado el valor directo e indirecto de la ictiofauna mediante el análisis de la captura de pescado adulto en el estuario y la dinámica de la población juvenil. Esto es de relevancia para la determinación del valor ecológico del recurso.

El modelo también fue usado para probar el impacto de diferentes escenarios de desarrollo en la población ictiológica, el potencial incremento en la carga nutricional debido al crecimiento urbano en la costa sur del estuario, comparado con la situación de referencia, así como el impacto que producirán cambios en la población inicial sobre la producción de peces.

Palabras clave: Modelación ecológica, pez, dinámica de población, estuario, aguas costeras, gestión.

INTRODUCTION

The simulation of higher trophic levels in the sea is important for several reasons: to provide a comprehensive description of the food web; to give an evaluation of the fish life-cycle and an estimation of the fish stock and fishery production; to try to improve diagnosis and prognosis of ecosystem trends; and to assist decision-makers. Knowledge of fish behaviour and interannual stock variations are important tools for effective fisheries management (Haedrich, 1980; Borja *et al.*, 1996; Motos, 1996). However, fish models are usually based strictly on population dynamics (e.g. stock-recruitment models) and thus cannot respond to changes in environmental forcing functions, other than implicitly. A lower recruitment level to a particular fishery will result in a stock reduction, but the reduction in recruitment may be caused by shifts in the breeding population (e.g. due to emigration), lower larval survival rates (e.g. due to temperature shifts), lower egg production (e.g. due to xenobiotics), or reduced growth (e.g. due to reduced food supply). Population models' lack of dependence on external forcing leads to a lack of response to its change, and severely limits their predictive capacity.

In order to develop a pelagic trophic chain model it is necessary to simulate nutrients and phytoplankton, zooplankton and nekton stocks; however, at the higher levels of the trophic pyramid the information available and understanding of processes is less complete. This is particularly true with fish behaviour, which is dominated by swimming and population dynamics processes, such as spawning, recruitment and larval development, which are not well understood, and result in stock variations on an interannual scale that make prognosis difficult (Balon, 1984; Houde, 1987; García and Palomera, 1996). Fish pass through different stages and successively display behaviour of suspended particles (eggs and yolk-sac larvae), zooplankton (larvae and early juveniles), and finally nekton (older juveniles and adults).

Because the spawning stocks of today determine the fish biomass of tomorrow, understanding the way those stocks are regulated may contribute to a better management of fish stocks. The task is complicated, because the biomass of individual fish species varies not only from year to year (through variation in year-class strength, due to a variety of causes), but also over long periods. The relation-

ship between stock recruitment and fishery stocks is non-linear, and the factors that regulate them are not directly correlated (Lett and Kohler, 1976; Mohn, 1991; Myers, 1991). These variations in larval recruitment will also affect long-term fluctuations. Larval transport away from favourable nursery areas and mass starvation of larvae at the time that feeding must be initiated are potential causes of extreme variations in year-class strength; other factors are transport mechanisms, oceanographic retention mechanisms, and spawning periods (Graham, 1972; Houde, 1987; Ré, 1994). These variations may be computed, based partly on observations.

The approach taken in the present paper consists of simulating the dynamic aspects of fish behaviour (including early life stages that are regulated by physical processes, and the swimming of juveniles and adults, which redistributes biomass in the estuary) and associating them with the trophic behaviour at each life stage in the food web of a macrotidal estuarine ecosystem. An estuary was chosen for the implementation of the model, for several reasons: firstly, estuaries are known to be very important for spawning, recruitment and larval development of fish (Ré, 1979; Norcross and Shaw, 1984; Houde, 1987), and thus for the maintenance of commercial offshore stocks of fish. Secondly, the fish population within an estuary may be more suitably modelled in a first approach than an offshore stock. The timing of biomass flux (input and output) across the system end-members is better understood than movement in the open sea, and biomasses for certain species are often high. Finally, physical processes may be represented with a simple advection-dispersion model, and the effects of changes to anthropogenic sources of organic matter (effluents) and river loading may be easily incorporated.

The general aim of this research was to develop a simulation of a pelagic fish population –incorporating known dependencies (e.g. feeding and growth), taken from the literature (Ré, 1979; Wootton, 1990), and areas of speculation (e.g. spawning and swimming) for which knowledge and data are incomplete– and to use it as a tool for analysing the interactions between higher trophic levels and their host ecosystem.

The specific objectives of this research were to develop a model for simulating a fish population in a macrotidal estuary, in order to reproduce the

stock recruitment with different year-classes; to integrate the fish model into a large-scale ecological model, and to analyse the system's response to different scenarios for initial fish stocks, fishing pressure and organic pollution.

MATERIALS AND METHODS

Description of the system

The model was built for the Tagus estuary (figure 1), but it can be applied to coastal waters generally. The Tagus estuary is the largest estuary on the west coast of Europe, with a surface area of 320 km² and a mean volume of $1\,900 \times 10^6$ m³. It receives freshwater discharges principally from the Tagus River, and pollutant discharges from many effluents. Tides are semi-diurnal (tidal range \approx 1 m at neap tide to \approx 4 m at spring tide), resulting in a large intertidal area of about 130 km² (Calvário, 1984; Cabrita and Moita, 1995).

The Tagus estuary comprises a deep, straight, narrow inlet channel and a broad, shallow inner bay. The inlet channel is 15 km long and 2 km wide, reaches a depth of 40 m, and constitutes the deepest part of the estuary. The inner bay (25 km long and 15 km wide) has a complex bottom topography with channels, tidal flat areas and sand banks, and has a mean depth of about 3 m (Calvário, 1984; Cabrita and Moita, 1995).

There is high primary productivity (Cabrita and Moita, 1995; Duarte and Ferreira, 1997; Ferreira, 1995) due to high incoming organic loads, which promote increased productivity at all trophic levels. Some additional information on nutrient loads

and concentration and plankton biomass and productivity are given in table I. Pollution is mainly due to bacteria and nutrients from the wastewater of Greater Lisbon, and localised industrial discharges. Although some persistent pollutants are accumulated through the food chain, the estuary remains an important area for the life cycles of many animals and for human exploitation of renewable resources.

Description of the fish population

A fish model has been developed and integrated into a large-scale ecological model. It was necessary to find a species that had a generic behaviour and could be used as a fishery resource, as a reference for other species. The most abundant pelagic fish of the Tagus is the anchovy *Engraulis encrasicolus* (Linnaeus, 1758), a marine species that enters the estuary to spawn (Ré, 1994; Motos, 1996), and which is important for fisheries. Globally, the fishery produces 30 000-40 000 t of anchovies annually in the Bay of Biscay (Borja *et al.*, 1996; Massé, 1996; Uriarte *et al.*, 1996). Anchovies are abundant in most European waters, from the Atlantic coasts (Borja *et al.*, 1996; Massé, 1996; Motos, 1996; Uriarte, Prouzet and Villamor, 1996) to the Mediterranean Sea (García and Palomera, 1996), and they constitute one of the single largest fisheries worldwide.

E. encrasicolus is a good example of a small pelagic species, it has a short life span (max. 3-4 years), active seasonal migrations to more productive areas, high fecundity (Motos, 1996), intense growth, early maturity (after its first year), schooling behaviour (especially in spring during the spawning sea-

Table I. Nutrient loads and initial concentrations of the different state variables of the model: dissolved inorganic nitrogen, ammonia, phytoplankton zooplankton and nekton. (*): includes Tagus River load

	Upper estuary* (Box 1-7)	Middle estuary (Box 8-10)	Lower estuary (Box 11-13)
Loads			
Nutrient loads (tons N year ⁻¹)	13 089	1 576	1 936
Concentrations			
Dissolved inorganic nitrogen ($\mu\text{mol N m}^{-3}$)	43.5	25.0	17.5
Ammonia ($\mu\text{mol N m}^{-3}$)	16.2	10.5	7.1
Phytoplankton biomass (mg Chl- <i>a</i> m ⁻³)	11.1	7.2	5.3
Zooplankton biomass (mg fresh weight m ⁻³)	3.4	4.8	7.9
Nekton biomass (mg fresh weight m ⁻³)	24.9	20.8	14.8

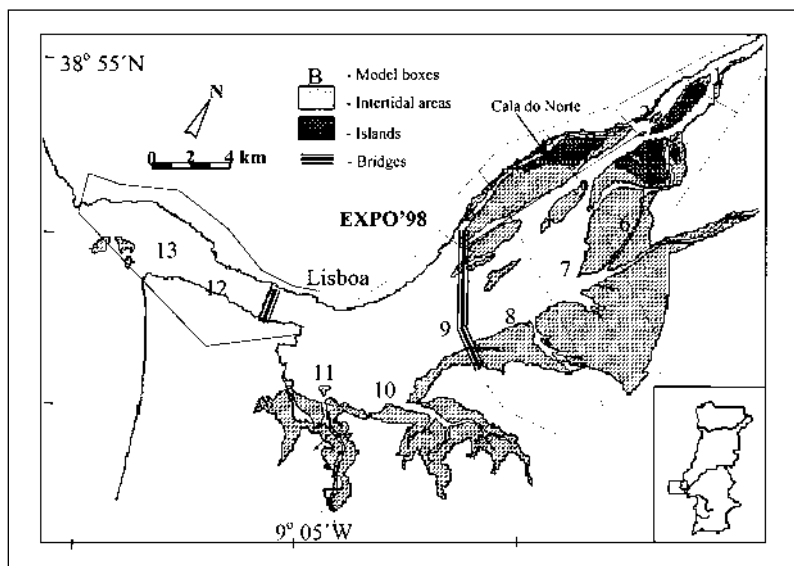


Figure 1. The Tagus estuary area, showing model boxes and intertidal areas

son) and high pelagic swimming activity (Uriarte, Proucet and Villamor, 1996). The mean adult size (standard length) is about 15 cm for a mean weight of 40 g. Its feeding regime is opportunistic, based mainly on zooplankton and, to some extent, on phytoplankton. In the Tagus, the spawning period appears to be between March and June (Ré, 1979). Each female produces on average of 200 000 pelagic eggs (Motos, 1996).

Description of the modelling approach

The present model (EcoWin) has been built using an object-oriented approach, which has several advantages for this kind of implementation; a full description of the model has been published elsewhere (Ferreira, 1995; Duarte and Ferreira, 1997). Ecological systems can be described in a much more natural form using an object-oriented programming (OOP) approach, and the different objects may interact with each other in different forms, offering great flexibility in the simulation (Ferreira, 1995). One of the most useful features of OOP is the ease with which major changes in models can be introduced with a minimum of recoding (Silvert, 1993). Thus, an OOP language can model the complex fishing-ground environment very flexibly and simply (Sekine, Nakanishi and Ukita, 1991).

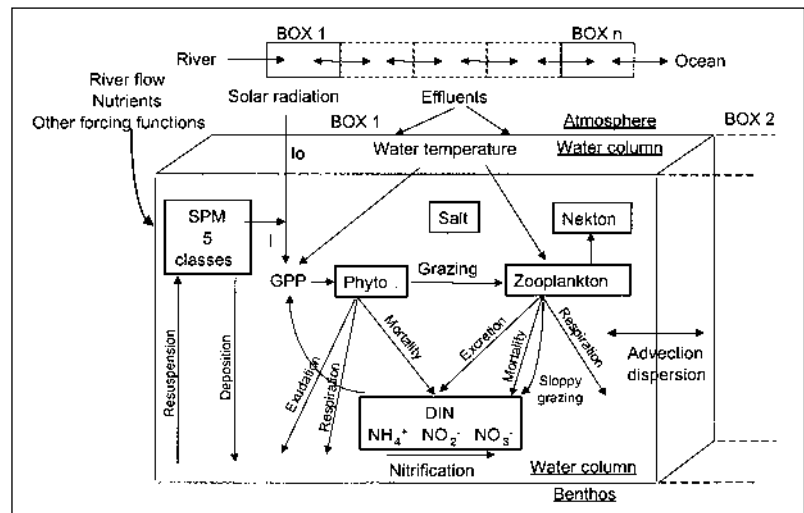
EcoWin uses OOP to simulate processes in an aquatic ecosystem. It is designed for modular construction of an ecosystem, model analysis and simulation of the system, prediction of the evolution of

an ecosystem, based on changes in its components, and real-time addition and removal of ecosystem compartments to test system response (Ferreira and Duarte, 1994). The program acts as an interface between a modelled ecosystem and users, who are able to select the objects they want to test, and to easily modify initial conditions, parameters and forcing functions.

The overall structure of the ecological model is shown in figure 2, and has been described previously (Ferreira, Duarte and Ball, in press). In brief, for the Tagus estuary, the model framework is that of an Eulerian box model, consisting of 13 boxes. The exchange between boxes is, for pelagic objects, dependent on the advective flow imposed by freshwater inputs to the system and the diffusive exchanges between the boxes.

The Tagus estuary model implemented in EcoWin is a one-dimensional, vertically integrated box model, within which the physical transport drives the biological processes and the biogeochemical sub-models interact with each other (Ferreira, 1995). The ecological objects built into the model include salinity, dissolved nutrients, phytoplankton, zooplankton and suspended particulate matter. Forcing functions and boundary conditions include river and effluent loading, freshwater discharge, tidal exchange, light and air temperature. The state variables are read by EcoWin at start-up and provide the system with data on the initial conditions for the simulation. Each object contributes with its state variables to the model,

Figure 2. General scheme of the Tagus ecological model. (Io): solar radiation at the sea surface; (I): underwater radiation; (GPP): gross primary production; (DIN): dissolved inorganic nitrogen



and can be switched on or off for different simulations.

Modelling the fish stocks

The conceptual approach of the nekton sub-model, which has been added to the global framework, is presented in further detail in figures 3 and 4. Figure 3 shows all the functions that regulate individual adult biomass and which are applied to the larvae and juveniles (Houde, 1987; Hinckley, Hermann and Megrey, 1996). Fish growth is influenced by the availability of adequate food, water temperature, and changes with age of the species. Recruitment is a complex process, depending on the size of spawning stocks and mortality of eggs and larvae, mainly caused by predation or environmental conditions. Mortality is high during the early life stages. Adult fish mortality has different causes (spawning stress or diseases from old age), and may be density-dependent. When food resources become insufficient death, by starvation may occur. Migrations, inputs or outputs in a given water mass or region are also modelled.

The general equation used to describe the fluctuation of the biomass was based partly on Sekine, Nakanishi and Ukita (1991):

$$\frac{dB}{dt} = G + L - (D + E + R + S) \pm M \quad [1]$$

where B = biomass, G = growth, L = recruitment, D = death, E = excretion, R = respiration, S = spawning, and M = migration.

Fish growth follows a Michaelis-Menten equation, essentially depending on the amount of food present in the box and on the temperature, with a threshold for feeding or, in other terms, of a density-dependence for prey:

$$G = G_{\max} \frac{\frac{P - P_0}{W_f}}{K_s + \left(\frac{P - P_0}{W_f} \right)} \quad [2]$$

where G_{\max} = maximum growth rate (depending on temperature), P = zooplankton biomass, P_0 = minimum feeding threshold, W_f = weight of fish, and K_s = half-saturation constant.

The larvae are also assumed to eat phytoplankton, and their growth is based upon the Ivlev equation (Ivlev, 1945):

$$R = R_{\max} (1 - e^{k(P_0 - P)}) \quad [3]$$

where R = ration, R_{\max} = maximum ration, and k = grazing constant.

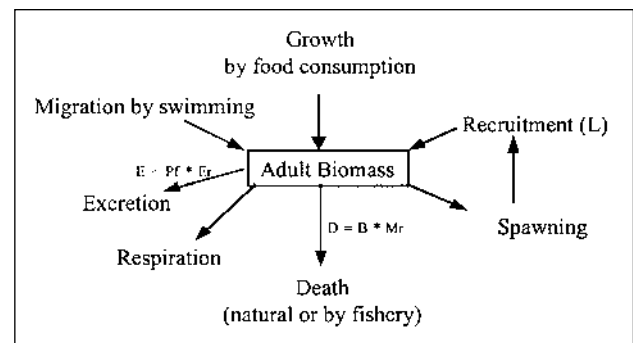


Figure 3. Functions regulating individual biomass (see text for equation symbols)

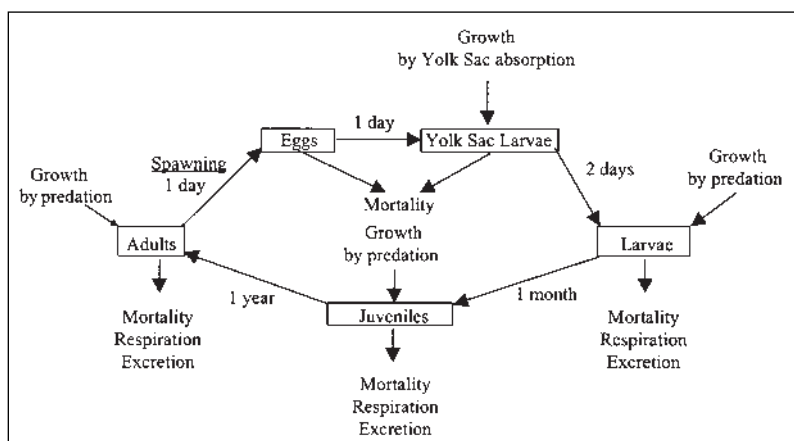


Figure 4. The life-cycle and main functions regulating the population stock

Because the model does not presently use a detrital compartment for remineralisation of detritus, the dead fish and unassimilated food, eliminated as faeces by fish, are assumed to be recycled instantaneously into the system as ammonia. Similarly, excretion of metabolically assimilated food as dissolved waste products (equation [4]), respiration (dependent on the energy used for feeding) and death (equation [5]), decrease the biomass (death and respiration) or the net production (excretion or faecal activity):

$$\mathbf{E} = \mathbf{P} \mathbf{f} \times \mathbf{E}_r \quad [4]$$

$$\mathbf{D} = \mathbf{B} \times \mathbf{M}_r \quad [5]$$

where Pf = fish production, and Mr = mortality rate.

Because there is little data concerning the nekton biomass in the estuary, the initial conditions for the simulated anchovy population were established as a proportion of the zooplankton biomass. Data from Kaizeler (1996) were scaled down, considering a ratio

$$\frac{\text{Energy extracted from a trophic level}}{\text{Energy supplied to a trophic level}}$$

of 0.1 (Parsons, Takahashi and Hargrave, 1984).

To simplify stock management, and considering data from Ré (1979), it is assumed that the entire *E. encrasicolus* population spawns on the same day (1 April of each year, Julian day 90). Thus, the adult population will lose its spawning biomass at the same time, and all the eggs will be released on the same day (i.e. the maximum difference in age will be of some hours). Each year-class proceeds from eggs to yolk-sac larvae, to larvae and juveniles at the end of the year. The latter are now able to

spawn and increase the adult stock (figure 4). In the model, larval recruitment was made directly proportional to the biomass of spawners. The biomass of the different life stages is linearly related to the mass of adult fish in each model box, and the life stages can appear in that box even if their stage duration is ended. The egg stage duration is one day, after which eggs become yolk-sac larvae, although some stay in the model ecosystem for 5 to 10 days and do not develop into the next life stage. These are considered non-viable, and will be remineralised into dissolved nutrients. This approach was applied to all year-classes.

It is assumed that eggs, yolk-sac larvae and larvae cannot move effectively (i.e. they exhibit planktonic behaviour) and that they are transported passively by the river flow and the tides, and redistributed through the whole estuary. Swimming activity for adult fish and juveniles has been implemented following Sekine, Nakanishi and Ukita (1991), based on fish preferences for food, depth, temperature and salinity. This method permits the redistribution of adults and juveniles based mainly on food availability. The parameters used for the simulation are given in table II.

EcoWin makes it possible to simulate different scenarios and compare them to the fish production of the standard model. The first scenario we used was the standard model; the second simulated an increased organic pollution load (represented as nutrient input); and the third and fourth scenarios simulated different initial fish biomass: 10 times the standard model, which could represent the entire fish population of the estuary, and 50 times, which could be an exceptional year-recruitment result. These scenarios were both tested with and

Table II. Parameters used in the model. The growth rates are in mg fw m⁻³ year⁻¹; other coefficients have no units

Adults		Early life stages	
Maximum adult growth rate	0.0123	Yolk-sac larvae growth rate	0.2
Growth rate at constant temperature	0.0693	Yolk-sac larvae mortality rate	0.29
Half-saturation constant	0.2	Maximum larval growth rate	0.25
Faecal rate	0.125	Larval growth rate at constant temperature	0.0693
Excretion rate	0.1	Larvae mortality rate	0.18
Respiration rate	0.0154	Maximum juvenile growth rate	0.009
Respiration rest rate	0.3	Juvenile growth rate at constant temperature	0.0693
Mortality rate	0.005	Juvenile mortality rate	0.01

without fishing pressure, based on a 5 % capture rate taken from the fish production.

RESULTS AND DISCUSSION

Response of the system

Table III compares the responses of the system with or without the nekton part of the ecosystem. The fish contribution is not very significant in terms of concentration, but considering the volume of the estuary, there is an important mass change. Excretion, faecal activity, respiration and death of adults, larvae and juveniles contribute with some ammonia, but this amount is trivial compared to the amount already present in the water, and loads to the estuary from other sources.

The model runs which include the fish show increased ammonia in the water column due to excretion and death, and a decrease in zooplankton biomass due to predation: this is in agreement with the results of other studies (e.g. Oviatt, Gall and Nixon, 1972). Predictably, reduced grazing pressure by the zooplankton leads to higher phytoplankton concentration. Even under high predation by larvae, juve-

niles and adults, the zooplankton decreases only marginally (about 5 %), which indicates that there is a lack of top-down control in the system.

Population dynamics of the fish stock

The simulation shows the successive life stages and the biomass of each year-class (figure 5). Each life stage begins with spawning or transfer from the previous stage, and a decrease by mortality or after the transition to the next stage. The variations in eggs and yolk-sac larvae biomass are similar, because mortality is the only process considered. Larvae and juveniles have different behaviour because of their metabolic activities. There is no growth for eggs, and yolk-sac larvae have a low rate because they eat their own yolk-sac resources, whereas larvae and juveniles have high growth curves, since the zooplankton threshold is not limiting in spring. Figure 5 shows only the results of the middle estuary, but the nekton biomass is distributed throughout the estuary by currents and swimming activity. The swimming of juveniles is questionable for younger juveniles, considering that their size cannot help them to resist the

Table III. Average values of nutrients, phytoplankton and zooplankton for the entire estuary of the standard model, with or without fish

	Without fish	With fish	Percentage change (%)
Ammonia ($\mu\text{mol N m}^{-3}$)	5.29	5.52	4.3
Phytoplankton ($\text{mg Chl-}a \text{ m}^{-3}$)	8.03	8.45	5.2
Zooplankton (mg FW m^{-3})	37.49	35.70	-4.8
Mass change			
Ammonia (kg N year^{-1})	140 714	146 832	6 118
Ammonia equivalent (kg C year^{-1})	904 590	943 920	39 330
Phytoplankton (kg C year^{-1})	433 995	561 925	27 930
Zooplankton (kg C year^{-1})	4 744	4 517	-227

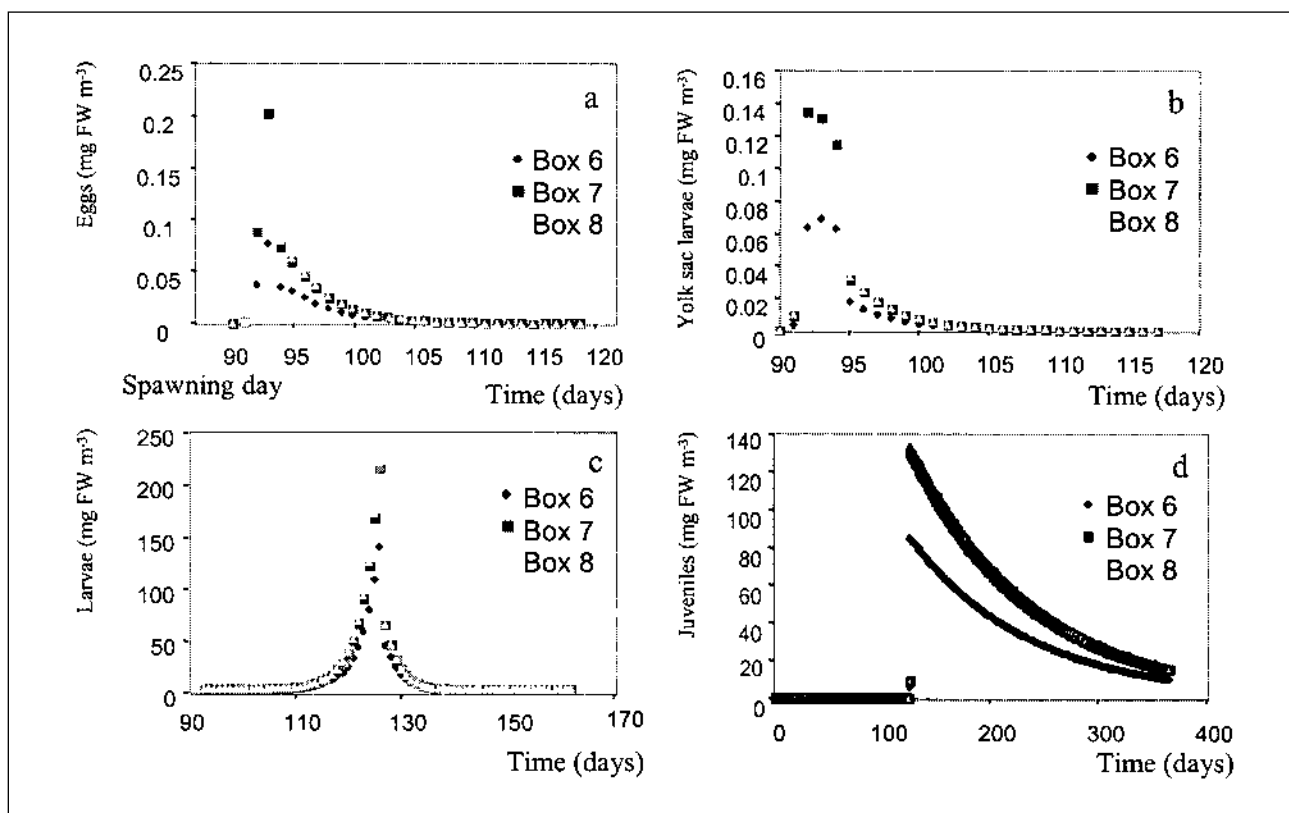


Figure 5. Simulation of life-stages of a pelagic fish

strength of the currents: a subdivision into size-classes, in progress, will improve this description.

As the zooplankton response with fish is not significantly different (table III), and shows no top-down control, the nekton object is not very sensitive to the increased organic pollution scenario (table IV). As expected, fish production increases with the increase of initial values, but this response is non-linear. Fishing pressure takes between 74 % and 77 % of the production and gives an idea of the potential annual fish catch for the entire estuary, which varies from 115-641 t per year, corresponding to an annual direct resource value of up to 640 000 euros. Fishing pressure decreases the production non-linearly, due to the nature of the

relationship between production and basic metabolism functions. In the third and fourth scenarios, fish production doubles for a five-fold higher initial value.

The different life stages in the early life history of fish make it possible to follow the periods of abundance and the general behaviour of the stocks, and provide information about their life cycle. The model shows the range of fish life-cycle variability, and can be extrapolated, to some extent, to other pelagic species.

During the sensitivity analysis, some non-specific parameters (e.g. excretion, respiration or faecal production rates), unrealistic parameters (e.g. instantaneous mortality rates), or non-existent ones

Table IV. Average values of fish production, in tons of fresh weight per year for the whole estuary, in different simulation scenarios. The income in euros is based on a dockside cost of 1 000 euros t⁻¹ fresh weight

Scenario	With fishing	Without fishing	Fishing mortality	% Fishing	Income (euros year ⁻¹)
Standard model	36	151	115	76	115 318
Nutrient loading	39	169	130	77	130 070
×10 Initial fish stock	118	460	342	74	341 914
×50 Initial fish stock	202	843	641	76	640 924

(spawning stress and senescence) were identified: these were used with caution. In particular cases (e.g. literature-based instantaneous mortality rates of 16-99 % for adults resulting in fish extinction in 1 year), the discrepancies identified led to modifications in order to calibrate the model. An analysis of the reasons for these differences may be a useful focus of research emerging from this research. Although the model cannot provide the correct values, it helps to examine the consistency of the parameters, and indicates a range within which these may be situated. The incongruity between the field measurements of parameters such as mortality and model requirements forces us to constructively analyse not only the model's conception and formulation, but potentially the available experimental data, as well.

The integration in this model of physical transport, biogeochemical processes, fish life-cycle, adult swimming and production is an innovative approach to fish modelling. It has enabled us to create a scenario analysis where effects of specific variables (e.g. organic load, stock increase) may be observed directly, rather than only indirectly, as in population dynamics approaches. With further development, this model may be used to provide some measure of the impact of estuarine nursery areas on offshore waters due to the export of juveniles, the seasonal dynamics of migratory species, and the body burden of xenobiotics in commercial species.

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